

BIOGEOCHEMICAL CYCLING AND NET PRIMARY PRODUCTION IN FOREST ECOSYSTEMS

EFFECTS ATTRIBUTED TO TWO DIFFERENT TREE
SPECIES, STAND AGE, LEAF CONSUMPTION BY
HERBIVORES AND SOIL ACIDIFICATION

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Lund 1977

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leaf consumption by herbivores and soil acidification.

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Fil kand., Sm.

Akademisk avhandling som för avläggande av filosofie
doktorsexamen vid matematisk-naturvetenskapliga fakul-
teten vid universitetet i Lund kommer att offentliggen
försvaras å Avdelningen för Ekologisk Botanik, östra
Vallgatan 14, Lund, torsdagen den 12 maj 1977 kl. 10.00.

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Efter lövsprickningen: den långa perioden av mogen, statisk grönska.
Nästan omärkligt bleks bladen tills de första roststänken tänder sina
signallampor. När dagarna krymper och solljuset mattas, avvecklas
driften successivt i lövens klorofyllfabriker.

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Lövfällningen - så enkel och så lätt den är! En resa i självklarhet
mellan de osynligheter ur vilka trädet bygger upp sitt liv: mellan den
strålning från rymden som kronan druckit och de jordens salter som
genom rötterna sugs mot höjden och som de singlande bladen ska åter-
förenas med.

Lövfällningen är trädens avbetalning på sina lån från jorden.

Ur "Vid trädets fot." - Rolf Edberg.

Enten:

När våren väcker bokens löv och sav i grenar stå,
när ljus far vildskogsbäcken och när vind på höjden rår,
när steg tas ut, man andas djupt, och bergen står i brand,
vänd åter, kom igen till mig! Så fagert är mitt land.

Ur "Sagan om de två tornen". - J.R.R. Tolkien.

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This thesis is based on the following three papers:

- I Nilsson, I. 1977. The influence of a leaf-eating insect (*Dasychira pudibunda* L. Lepidoptera) on internal plant nutrient transports and tree growth in a beech forest (*Fagus sylvatica* L.) in southern Sweden - Submitted to *Oikos*.
- II Nilsson, I., Nihlgård, B. and Staaf, H. 1977. Tree biomass, net primary production and litter fall dynamics in three adjacent spruce plantations in South Sweden. - Technical report, Avd. Ekol. Bot., Lunds Univ. 23 pp.
- III Nilsson, I. 1977. The acidification sensitivity of some Swedish forest soils - Meddn. Avd. Ekol. Bot., Lunds Univ. 32. 84 pp.

INTRODUCTION

Studies of the biogeochemical cycling in forest ecosystems may have many objectives, among which the following ones should be stressed:

- 1) a quantification of the ability of the system to retain biogeochemical elements.
- 2) a quantification of the ability of the system to recycle biogeochemical elements within the system.

Information can be obtained from studies of:

- a) intact systems
- b) systems which have been subjected to a natural perturbation (fire, overexploitation by herbivores etc)
- c) deliberately perturbed systems (e.g. by reforestation with a new tree species, fertilization, liming or acidification of the soil etc)
- d) more or less complete laboratory systems, which can be manipulated under strongly standardized conditions.

The aims of the present work are to evaluate:

1. The recycling of elements in spruce plantations of different age.
2. The recycling of elements in a 90-year-old beech forest subjected to overexploitation by herbivores.
3. The base cation retaining capacity of forest soils when exposed to strong acid.
4. The influence of alterations in retaining and recycling processes on net primary production.

The information is obtained in the following manner:

Intact system	Perturbed system	Investigated variables
90-year-old beech forest Maj 1971-April 1972 (I)	The same forest subjected to an overexploitation by herbivores (<i>Dasychira pudibunda</i> <i>Lepidoptera</i>) in 1972-1973	Structural composition and amounts of litter fall; L. contents of biogeochemical elements in litter fall; contents of biogeochemical elements in throughfall precipitation.
- " - (II)	Spruce plantations of different age on former beech forest soil. Investigation period: 1971-1974	Structural composition and amounts of litter fall; contents of biogeochemical elements in litter fall.
Soil samples from 22 forest ecosystems in southern Sweden (III)	The same samples treated with defined amounts of strong acid	Bonding strength at the colloid surfaces, tested for Ca, Mg and K. Acid buffer capacity; Cation exchange capacity; Base saturation and base cation saturation; Humus content and clay content.

The elucidation of biogeochemical cycling is not a goal in itself, but should be treated as one subset of variables regulating the occurrence and fitness of the organism populations.

As far as plants are concerned fitness could be tested e.g. by measuring reproductive potential or net primary production. The latter approach has been adopted in the present study.

GROWTH DEVELOPMENT IN THE BEECH FOREST AND THE SPRUCE STANDS

Net primary production and tree biomass were in the range of $13 \text{ ton} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$ and $300 \text{ ton} \cdot \text{ha}^{-1}$ respectively both in a 70-year-old and a 40-year-old spruce stand. These figures were fairly similar to those found in the beech forest, ca. $14 \text{ ton} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$ and $330 \text{ ton} \cdot \text{ha}^{-1}$, a tendency which is in accordance with that found by Nihlgård (1972), who compared another plot in the beech forest with an adjacent 55-year-old spruce stand. In the present study two growth revisions were made with a time interval of 30 months. Despite rather wide 95% confidence limits, the data, including those of a 15-year-old spruce stand, suggest a biomass increment corresponding to three years net primary production minus litter fall. The 15-year-old spruce stand revealed the most vital growth development, shown by its P_N/B -ratio of 0.10. The corresponding ratios for the two oldest spruce stands and the beech forest were in the range of 0.040-0.045. Net primary production was ca. 15 and 19 $\text{ton} \cdot \text{ha} \cdot \text{year}^{-1}$ in February 1972 and August 1974 respectively. Corresponding figures for tree biomass were 146 and 181 $\text{ton} \cdot \text{ha}^{-1}$. Nevertheless it could be suspected that the growth conditions in the two youngest spruce stands were somewhat suboptimal due to high stocking densities. The 15-year-old stand suffered a high tree mortality between the two growth revisions, ($800 \text{ trees} \cdot \text{ha}^{-1} \cdot 30 \text{ months}^{-1}$).

AMOUNTS OF LITTER FALL AND THE CORRESPONDING FLUXES OF BIO-GEOCHEMICAL ELEMENTS IN THE BEECH FOREST AND THE SPRUCE STANDS

Litter fall was $4.4 \text{ ton} \cdot \text{ha}^{-1}$ in the beech forest during the period May 1971-April 1972, compared to $3.0 - 5.5 \text{ ton} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$ in the spruce stands. Fluxes of biogeochemical elements in litter fall were quantified in the 70-year-old and the 15-year-old spruce stands, being significantly higher in the latter one due to high litter fall amounts and element

concentrations especially in needle fall. The high stocking density (5800 trees.ha⁻¹ in 1974, compared to 576 trees.ha⁻¹ in the 70-year-old stand), certainly caused a substantial premature needle fall due to light deficiency at the lower branches. An insufficient withdrawal of for instance N, P and K could explain the high concentrations, that were actually found.

The element fluxes in the litter fall of the beech forest during May 1971 - April 1972, were similar to those of the youngest spruce stand. They seemed to proceed at a slower rate in the oldest spruce stand. However, according to Nihlgård (1972) a summation of fluxes in litter fall and stand precipitation yield figures that are higher in a mature spruce stand than in the beech forest. It is still an open question, however, whether the main amount of biogeochemical elements in stand precipitation emanates from canopy leaching or from the washout of adsorbed aerosols.

INTERNAL PLANT NUTRIENT TRANSPORTS IN THE BEECH FOREST, SUBJECTED TO OVEREXPLOITATION BY HERBIVORES

A two-year population peak of the pale tussock moth (*Dasychira pudibunda* L. Lepidoptera), caused a steady decrease of annual leaf litter fall. Throughfall precipitation was enriched about three times with respect to N, P and K in 1973 compared to 1971. Significant differences between the annual fluxes of P, S, Cu, Mn, Ca, Mg, Na, K and N were found in the litter fall. The latter was mainly made up of green leaf frass and larval faeces in 1973, and to a minor extent so in 1972. Total litter fall turned out to be fairly similar during the whole investigation period (ca 4.5 ton.ha⁻¹.year⁻¹). No decrease of the net primary production was found, probably because the main leaf consumption takes place rather late in the season (in the middle of July or the beginning of August).

Besides, the forest is in a mature stage, where growth reductions might be difficult to reveal. There could also be a certain positive effect of the leaf consumption, like for instance an increased mineralization rate of nitrogen and phosphorous, due to the large contribution of leaf frass and faeces to total litter fall. On the other hand an increased leaching of potassium should be expected (cf. Kimmins 1972, Rafes 1970).

CATION LEACHING FROM SOILS CAUSED BY ACIDIFICATION

Laboratory experiments (III) show that the bonding of base cations (Ca^{2+} , Mg^{2+} and K^{+}) to the soil colloid surfaces is most negatively affected by acidification in soils with low stores of exchangeable cations, calculated on a relative scale. This interpretation emanates from ion adsorption isotherms, the alterations of which, due to acidification are discussed in connection with an array of commonly measured physico-chemical variables like humus content, clay content, cation exchange capacity, base saturation, and metal saturation, which all can be taken as indirect measures of exchangeable base cation stores. Acid buffer capacity is strongly correlated with base saturation and the sum of base cations calculated on a dry weight basis, which indicates that the exchangeable cations are of crucial importance for maintaining the pH stability of a soil. Losses could of course be compensated in the long run by weathering processes, in which oxonium ions are actually neutralized. Soils with low stores of exchangeable base cations often have a low weathering capacity however. Applications of $100 \text{ kg sulfuric acid} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$, during six years in a pine stand on poor glacial sand, caused a reduction of the base cation stores in the mor layer and the upper ten centimetres of the mineral soil with more than 50 per cent (Tamm 1977). Thus weathering processes seem to be of minor importance in this experiment.

Statistical analyses performed by Dahl et al (1967), showed a positive relationship between base saturation and the nitrogen content of the humus layer in forest soils. As nitrogen is a limiting factor in forest ecosystems, one would suspect that a decreased base saturation due to cation leaching would cause a growth reduction of the forest trees. According to the available literature no such growth reduction has been found. However, it should be noticed that the period of increased atmospheric acid deposition (ca 25 years) is relatively short compared to the average tree generation time (ca 100 years).

CONCLUDING REMARKS

The two main themes of this thesis are the cycling rate of biogeochemical elements within forest ecosystems and the net primary production of trees. It is shown that the cycling rate can be affected by both abiotic and biotic perturbations. Due to homeostatic mechanisms within the system it is difficult to obtain direct cause-effect relationships between plant nutrient cycling and net primary production. This is most clearly illustrated in paper I. There also should be considerable time lags between an alteration of the cycling conditions and an observable reaction from the plant populations (cf. paper III).

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